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Synopsis of *Trichanthera* (Acanthaceae: Ruellieae: Trichantherinae)

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***Trichanthera* consists of two Neotropical species of shrubs and trees. *Trichanthera gigantea* is widespread in northern South America and Panama, whereas *T. corymbosa* is restricted to northeastern Colombia and northwestern Venezuela. The unusual pollen of both species is characterized and conforms to that of most other genera of Trichantherinae. Pollination of *T. gigantea* by bats has been documented, and other floral visitors to that species include hummingbirds, bees, and ants. A key to genera of Trichantherinae is followed by a generic description, key to species, species descriptions, and discussions. Local common names and uses are listed for both species. *Trichanthera gigantea* demonstrates potential as an important tropical forage crop, and its use in northern South America contributes to local sustainability. Preliminary conservation assessments for each species are proposed. Maps of geographic ranges and illustrations of each species are provided.**

***Trichanthera* consta de dos especies neotropicales de arbustos y árboles, uno de los cuales, *T. gigantea*, se encuentra en el norte de América del Sur y Panamá. La otra especie, *T. corymbosa*, se limita al noreste de Colombia y noroeste de Venezuela. El polen inusual de ambas especies se caracteriza y ajusta al de la mayoría de los otros géneros de Trichantherinae. La polinización de *T. gigantea* por murciélagos ha sido documentada, y otros visitantes florales para esta especie incluyen colibríes, abejas y hormigas. Una clave para los géneros de Trichantherinae es seguida por una descripción genérica, clave para las especies, descripciones de cada especie, y discusiones. Nombres comunes locales y usos se incluyen para ambas especies. *Trichanthera gigantea* demuestra potencial como un importante cultivo de forraje tropical, y su uso en el norte de América del Sur contribuye a la sostenibilidad local. Se proponen evaluaciones preliminares de conservación para cada especie. Se incluyen mapas de distribución geográfica e ilustraciones de cada especie.**

Trichanthera Kunth consists of two Neotropical species that occur in southern Central America and northern South America. Leonard (1930) provided a taxonomic synopsis of the genus in which both species and a variety of *T. gigantea* were recognized. The present account summarizes and augments morphological, geographical, ecological, and phylogenetic knowledge gained about *Trichanthera* during the past 85 years. The increasing use of *T. gigantea* as a forage crop in various parts of the world highlights the need for accurate information about these aspects of the genus.

Trichanthera has traditionally been treated in tribe Trichanthereae of subfamily Ruellioideae along with four other Neotropical genera (*Bravaisia* DC., *Sanchezia* Ruiz & Pav., *Suessenguthia* Merxm., and *Trichosanchezia* Mildbr.), all of which share the morphological synapomorphy of "loxodicolporate" pollen (Daniel 1998). Recent molecular phylogenetic studies reveal this assemblage (i.e., "core Trichantherinae") to be monophyletic and sister to the Neotropical (primarily

Mexican) genus *Louteridium* S. Watson (Tripp et al. 2013). All six genera were treated as subtribe Trichantherinae by Tripp et al. (2013). *Louteridium* differs from other Trichantherinae by numerous morphological distinctions (see key below), and was previously treated in its own tribe. The tree habit, which is rare among Acanthaceae, is probably best expressed in this subtribe. It occurs in both species of *Trichanthera,* as well as among species of *Louteridium*, *Suessenguthia*, and *Bravaisia*. Among core Trichantherinae, *Trichanthera* and *Bravaisia* are sister to the remaining three genera, which form a strongly supported "staurogynoid clade." Tripp et al. (2013) treated all six genera as Trichantherinae, one of seven subtribes of tribe Ruellieae. Taxonomic revisions have been provided for *Bravaisia* (Daniel 1988), *Louteridium* (Richardson 1972; Daniel and Tripp in prep.), *Sanchezia* (Leonard and Smith 1964), *Suessenguthia* (Wasshausen 1970; Schmidt-Lebuhn 2003), and *Trichanthera* (Leonard 1930). These genera, and unispecific *Trichosanchezia* (Mildbraed 1926), can be characterized and identified by the morphological attributes in the following key:

Key to Genera of Trichantherinae

1a. Calyx 3-lobed; corolla throat conspicuously gibbous-saccate ventrally; seeds 12–24 per capsule; pollen pantoforate . . . . *Louteridium*
1b. Calyx 5-lobed; corolla throat sometimes ampliate but not conspicuously gibbous-saccate ventrally; seeds up to10 per capsule; pollen loxodicolporate 2

2a. Corolla subcylindric (or at least with the tube subcylindric and elongate; or if with a ± ampliate throat as sometimes in *Suessenguthia multisetosa*, then with flowers borne in headlike involucres subtended by several pairs of bracts); fertile stamens 2 or 4. 3
2b. Corolla ± campanulate (i.e., throat ampliate; flowers not borne in headlike involucres as described above); fertile stamens 4 5

3a. Fertile stamens 2 . . . . *Sanchezia*
3b. Fertile stamens 4 4

4a. Thecae awned at base. . . . . *Suessenguthia*
4b. Thecae awnless . . . . *Trichosanchezia*

5a. Thecae awnless, rounded at base; capsule pubescent at maturity; flowers borne on pedicels 2–11 mm long; stigma 1.5–4.5 mm long . . . . *Trichanthera*
5b. Thecae awned with a single, subulate projection 0.3–1 mm long at base; capsule glabrous at maturity; flowers sessile or borne on pedicels to 2 mm long; stigma to 1 mm long. *Bravaisia*

Both species of *Trichanthera* exhibit the loxodicolporate pollen characteristic of the core Trichantherinae (Fig. 1). Grains can be characterized (with shapes, measurements, and ratios in parentheses based on data from Raj 1961) as globose-elliptic to globose-oblong, longer equatorial axis:shorter equatorial axis = 1.03–1.75, 2-colporate, polypseudocolpate, polar axis = 67–79 (–101) µm, equatorial axis of apertural face = 55–70 (–96) µm, equatorial axis of interapertural face = 40–62 (–83) µm, apertural face subcircular to broadly elliptic in outline, interapertural face broadly elliptic to oblong in outline, colpi and pseudocolpi microgemmate to gemmate, exine between colpi divided into bands by pseudocolpi, bands psilate and perforate to foveolate with a single and central row of round to elongate lumina 0.3–3.3 µm in diameter or long, portion of the 2 bands flanking ora protruding and liplike, sculptural features of one apertural face usually oriented ± 90° to those of opposing face. Roubik and Moreno P. (1991) described pollen of *T. gigantea* from Barro Colorado Island in Panama as "spheroidal" and 63–127 µm.

Although fossil pollen showing similarities to that of core Trichantherinae has been described

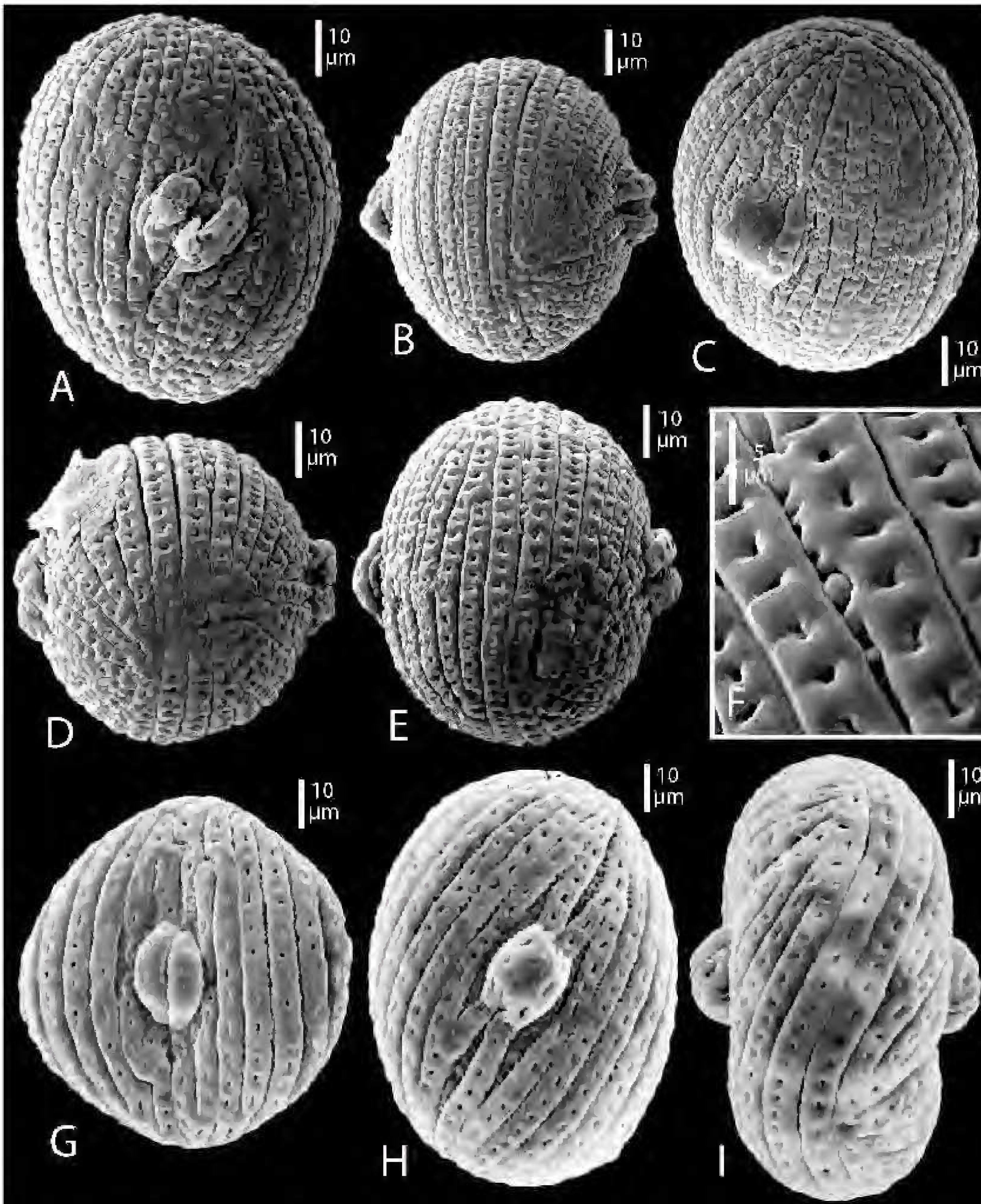

FIGURE 1. Pollen of *Trichanthera*. A–F. *T. corymbosa* (*Romero-Castañeda 10753*). A. Apertural view. B. Interapertural view with apertural faces oriented at ± right angles to each other. c. Subapertural view. D. Interapertural view of subradially symmetric grain. E. Interapertural view with apertural faces offset but oriented less than 90° relative to each other. F. Close-up of pseudocolpi and exine bands. G–I. *T. gigantea* (*Daniel et al. 5474*). G. Apertural view. H. Apertural view showing sculpturing of colpi and pseudocolpi. I. Interapertural view with apertural faces oriented at right angles to each other.

from both the Triassic (Pocock and Vasanthy 1988; North America, ca. 227–231 Ma) and Jurassic (Cornet and Habib 1992; Europe, ca. 157–163 Ma) periods of the Mesozoic era, the likelihood of highly derived angiospermous pollen from times as early as these would appear to be anomalous. Similar pollen from the Miocene has been used in dating analyses (Tripp and McDade 2014; q.v. for a ranking of the utility of various reports).

Elsewhere among Ruellieae, the normally 3-colporate and polypseudocolpate pollen of *Strobilanthes neilgherrensis* Bedd. (as *Nilgirianthus neilgherrensis* (Bedd.) Bremek.) in Strobilanthinae was observed to have several rare variants in aperture number and torsion of exinal features that included a single 2-aperturate grain with opposing faces ± 90° out of phase with one another (Vasanthy and Pocock 1986). These authors also noted the occurrence of rare transitional (i.e., with partially rotated hemispheres) grains, and very rare radially symmetric grains, among the otherwise loxodicolporate grains of *Bravaisia integerrima* (Spreng.) Standl. and *Sanchezia lampra* Leonard & L.B. Sm. Pollen of *Trichanthera corymbosa* examined here also varies from nearly radial to the rotated symmetry (up to 90°) common among Trichantherinae. Thus, variation in pollen of these species from two subtribes of Ruellieae likely provides insights into the origin of pollen characteristic of core Trichantherinae. Whereas the rare occurrence of loxodicolporate pollen in *S. neilgherrensis* appears to be anomalous, this type of pollen has become generally "fixed" among core Trichantherinae.

Trichanthera Kunth in Humboldt, Bonpland and Kunth, Nova Gen. Sp. 2:243. 1818 ("1817") (non Ehrenberg 1829). **Type.**— *Trichanthera gigantea* (Bonpl.) Nees (≡ *Ruellia gigantea* Bonpl.)

Trixanthera Raf., Sylva Tell. 146. 1838. **Type.**— *Trixanthera angularis* Raf., nom. illeg. (≡ *Ruellia gigantea* Bonpl.)

Shrubs or medium-sized trees with cystoliths, sometimes with multiple trunks and prop roots. Young stems quadrate-sulcate, often with warty or blisterlike tubercles on surface. Leaves opposite, petiolate, the pair at a node equal or usually unequal in size, blades subcoriaceous. Inflorescence of terminal thyrses (i.e., bearing pedunculate dichasia with pedicellate flowers) or, when branched, a terminal panicle of thyrses; each dichasium + peduncle subtended by a bract, each flower + pedicel subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes homomorphic or heteromorphic (4+1), imbricate during anthesis, sometimes elongating in fruit. Corolla ± campanulate, internally ± waxy or glossy, externally densely pubescent (except for proximal portion), tube funnelform with narrow proximal portion subcylindric and throat ampliate, limb 2-labiate or appearing ± actinomorphic, upper lip 2-lobed, lower lip 3-lobed, corolla lobes contorted in bud. Stamens 4, in two pairs, each pair consisting of a longer and a shorter stamen that are fused proximally, inserted at or near base of throat, exserted from mouth of corolla, extending beyond lips of corolla, longer stamen of each pair posterior and central in display of stamens, anthers 2-thecous, thecae of a pair equally inserted, parallel to subsagittate, rounded at base, lacking appendages, dehiscing toward lower lip (i.e., flower nototribic), pollen loxodicolporate. Style exserted from mouth of corolla, extending beyond lips, stigma asymmetric, usually exserted beyond anthers, 1 lobe ± vestigial. Capsule ellipsoid, estipitate, bearing retinacula. Seeds up to 10 per capsule, lenticular, surfaces smooth, shiny, and lacking trichomes.

The genus consists of two species and is native to southern Central America (Panama) and northern South America (Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, and Venezuela). Both species occur in moist to wet forests.

The generic name *Trichanthera* is nearly universally cited as having been published by Kunth in Humboldt, Bonpland, and Kunth's *Nova Genera et Species Plantarum* vol. 2, on page 243 (the quarto edition was published earlier, in February, than the folio edition, which was published in June, of 1818; the publication date listed on the printed copies was "1817;" Stafleu and Cowan 1979). In this publication, Kunth indicated that *Ruellia gigantea*, "certe distincti generis ob stamina exserta, antheras pilosas et capsulae loculos dispermos. Fortasse Trichanthera nominandum." Thus, he was indicating that the species was deserving of generic status and proposed "Trichanthera" as a possible name, but did not accept it in this publication. In 1829, Ehrenberg published *Trichanthera* Ehrenb. for an Old World genus of Zygophyllaceae (subsequently treated in Malvaceae and Sterculiaceae). This name has been treated as illegitimate due to the prior existence of Kunth's name. *Eurynema* Endl. was proposed by Endlicher (1842) as a new name for Ehrenberg's "illegitimate" name, but no combination was made for the sole species, *T. modesta* Ehrenb., which is now known as *Hermannia modesta* (Ehrenb.) Mast. (the combination for this name was effected by Masters in 1868, where the combination was attributed to Planchon, who instead made the combination *Mahernia modesta* (Ehrenb.) Planch. in 1855; *Mahernia* L. is sometimes treated as a synonym of *Hermannia*). However, if Kunth's name was not validly published, *Trichanthera* Ehrenb. becomes legitimate; it is currently treated as a heterotypic synonym of *Hermannia* L. The next generic name proposed for the acanthaceous species treated by Kunth was *Trixanthera* Raf., proposed by Rafinesque (1838) specifically for *Ruellia gigantea*, to which species he gave the name *T. angularis* Raf. If Kunth's generic name had been validly published, *Trixanthera* would be a synonym of it and *Trixanthera angularis* would be an illegitimate name and synonym of *Trichanthera gigantea*. Apparently, the first publication of the acanthaceous genus *Trichanthera* was that of Meisner (1840), who attributed the generic name to Kunth, but provided his own description. In 1847, Nees made the combination for the type, *T. gigantea* (Bonpl.) Nees

From the preceding summary, it is clear that *Trichanthera* Kunth is not validly published and that *Trichanthera* Ehrenb. has priority over *Trichanthera* Meisn. Without proactive nomenclatural actions (e.g., conservation), the oldest legitimate name for the genus containing *Ruellia gigantea* is *Trixanthera* Raf., and new combinations for *R. gigantea* and *T. corymbosa* in that genus would be necessary. It might be argued that Rafinesque's name should be considered an orthographic error ("trich" refers to hairs, "trix" refers to three-fold) for Kunth's name, and that he was, in effect, validating Kunth's proposed name. Were it not for Ehrenberg's publication of *Trichanthera* for the sterculiaceous genus nine years before Rafinesque's publication, this might have been a fortuitous argument to preserve the original spelling of Kunth's name.

A proposal for conservation of the acanthaceous name *Trichanthera* is currently being prepared for submission to the Nomenclature Committee for Vascular Plants of the International Association for Plant Taxonomy. Although incorrect, the traditional author citation for the genus is used herein in accordance with Recommendation 14A.1 of McNeill et al. (2012).

Key to the Species of *Trichanthera*

1a. Thyrse usually corymbose; calyx 14–24 mm long during anthesis, lobes heteromorphic with 1 lobe conspicuously longer and wider (ca. 1.5 × or more wider) than others, the four similar lobes linear to linear-elliptic to linear-lanceolate, 2–4 mm wide, acute at apex; bracteoles and secondary bracteoles oblanceolate to linear, 4–12 (–25) mm long . . . . 1. *T. corymbosa*

1b. Thyrse elongate; calyx 6–13 mm long during anthesis, lobes homomorphic and ± equal in size, ovate-elliptic to elliptic, 3.5–7.3 mm wide, rounded at apex; bracteoles and secondary bracteoles triangular, 2–4 mm long . . . . 2. *T. gigantea*

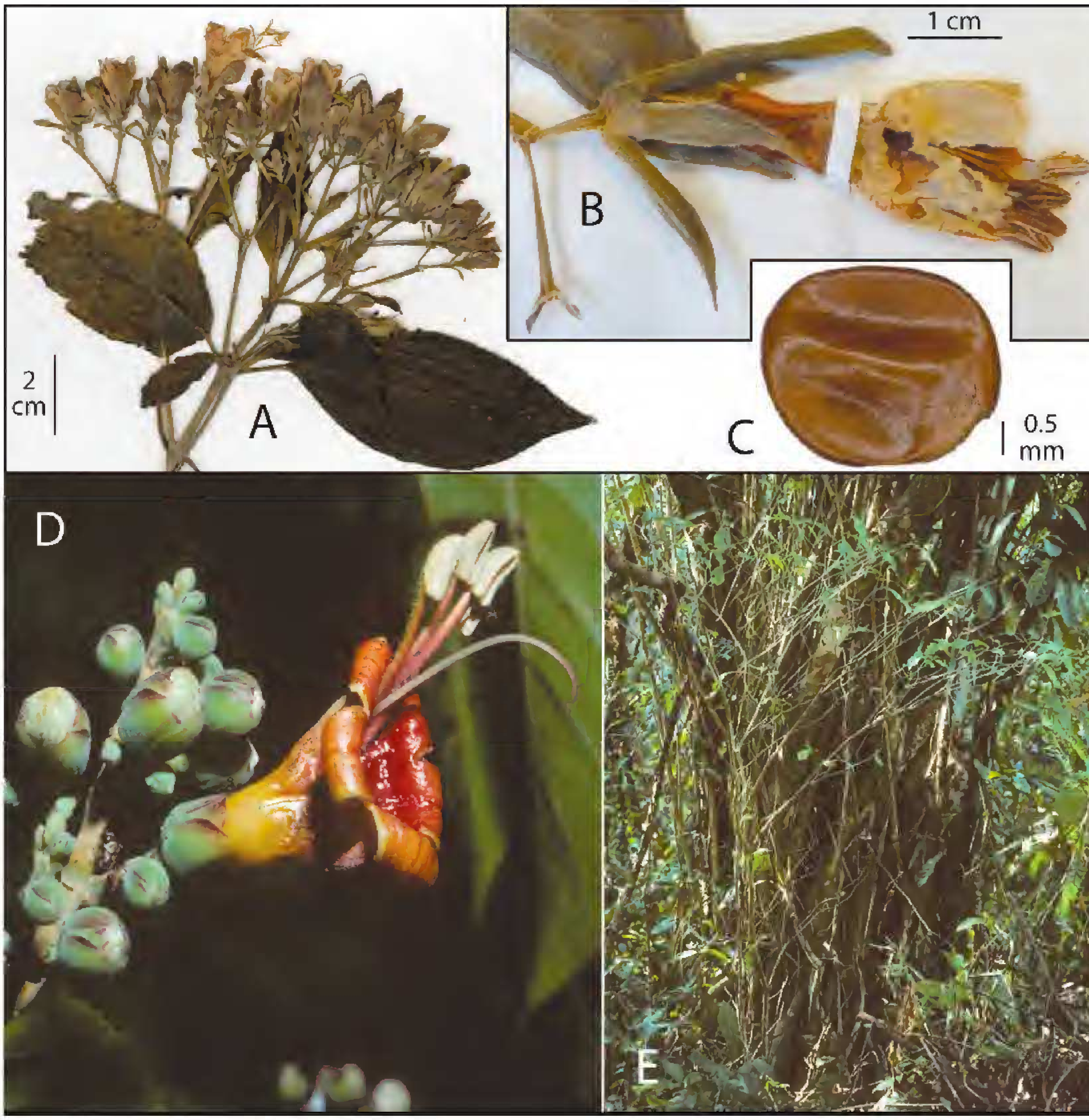

FIGURE 2. *Trichanthera corymbosa* (A–C) and *T. gigantea* (D, E). A. Corymbose inflorescence (*Romero C. 10753*, MO). B. Flower showing calyx with heteromorphic lobes (*Pittier 12828*, NY). C. Seed (*Trujillo & Fernández 16379*, US). D. Inflorescence and flower (*Daniel et al. 5474*). E. Base of tree with suckering (*Daniel et al. 5474*).

1. *Trichanthera corymbosa* Leonard, J. Wash. Acad. Sci. 20:487. 1930. **TYPE.**— COLOMBIA. **Norte de Santander**: Culagá Valley, near Tapatá (N of Toledo), 1500–2100 m, 3–8 March 1927, *E. Killip & A. Smith 20140* (holotype: US!; isotypes: BM!, GH-image!, NY!). Figure 2.

Trees to 20 m tall; young stems covered with sessile and lenticular glands to 0.05 mm in diameter (often inconspicuous; punctate-glandular) and puberulent with antrorse eglandular trichomes to 0.1 mm long, nodes sometimes with longer flexuose eglandular trichomes as well. Leaves petiolate, petioles to 45 mm long, blades ovate to elliptic to broadly elliptic, 33–265 mm long, 16–140 mm wide, 1.3–2.4 × longer than wide, rounded to cuneate at base, acute to acuminate at apex, surfaces punctate-glandular and sometimes with eglandular trichomes along major veins on abaxial surface, margin sinuate to sinuate-crenate. Inflorescence a terminal corymbose thyrse (or if basally branched, then a panicle of thyrses) 48–149 mm long, rachis punctate-glandular and pubescent with antrorse eglandular trichomes 0.05–0.2 mm long, dichasia expanded to a greater or lesser degree, pedunculate, peduncles to 55 mm long, pubescent like rachis, secondary peduncles similar to peduncles. Bracts often caducous, subfoliose and reduced in size distally, ovate to elliptic to oblanceolate to linear, 7–72 (–170) mm long, 2–34 (–80) mm wide, pubescent like leaves (proximal bracts) or rachis (distal bracts). Bracteoles and secondary bracteoles (subfoliose to) oblanceolate to linear, 4–12 (–25) mm long, 1–3.2 (–5) mm wide. Flowers pedicellate, pedicels 4–11 mm long. Calyx green with purplish tinge, 14–24 mm long during anthesis, tube 2–4 mm long, lobes heteromorphic (4 + 1), four similar lobes linear to linear-lanceolate to linear-elliptic, 8–19 mm long, 2–4 mm wide, acute at apex, fifth (posterior) lobe lanceolate to elliptic to oblong to obovate-elliptic, 12–27 mm long 4.5–8.5 mm wide, longer than and ca. 1.5 or more × wider than other lobes, rounded to acute to attenuate at apex, lobes with abaxial surface punctate-glandular and with eglandular trichomes like those of rachis, margin ciliate with similar eglandular trichomes. Corolla whitish to maroon or purplish (see discussion), (18–) 23–43 mm long, externally punctate-glandular and densely pubescent with retrorsely appressed eglandular trichomes to 0.5 mm long (except for proximal portion of tube which lacks eglandular trichomes), narrow proximal portion of tube 7–15 mm long, throat 8–18 mm long, 9–13 mm in diameter near midpoint, limb 18–34 mm in diameter, lobes oblong to broadly ovate to triangular, 6–12 mm long. Stamens ca. 20–27 mm long, filaments pubescent proximally with flexuose eglandular trichomes to 3 mm long and sometimes with glandular trichomes as well, sometimes glabrous or nearly so distally, thecae 4–6.5 mm long, (glabrous or) pubescent with flexuose eglandular trichomes to 1.5 mm long and on dorsal surface and connective also pubescent with sessile glands (≤ 0.05 mm diam.), pollen (*Romero-Castañeda 10753*) 72–74 µm (polar axis) × 55–60 µm (equatorial axis, apertural face) × 56–62 µm (equatorial axis interapertural face). Style 28–38 mm long, pubescent proximally, glabrous distally, stigma with 1 lobe straight, 1.5–4 mm long, other lobe vestigial, 0.05–0.2 mm long. Capsule 16–21 mm long, densely pubescent with straight to flexuose eglandular trichomes to 1 mm long. Seeds 3.6–4 mm long, 2.9–3.6 mm wide.

Phenology.— Flowering: October–March. Fruiting: October–March.

Distribution and habitats.— Northern South America (northeastern Colombia and northwestern Venezuela; Fig. 3). Plants occur along streams in moist to wet lowland to montane primary and secondary forests (including cloud forests) at elevations from 900 to 1800 m (possibly up to 2300 m fide Bono 1996). The distribution of this species occurs exclusively within that of the more widespread *T. gigantea*. Indeed, the two species of *Trichanthera* would appear to be sympatric or at least to grow in the near vicinity of one another; the type of *T. corymbosa* and a collection of *T. gigantea* were both collected at the same locality by Killip and Smith in the department of Norte de Santander, Colombia.

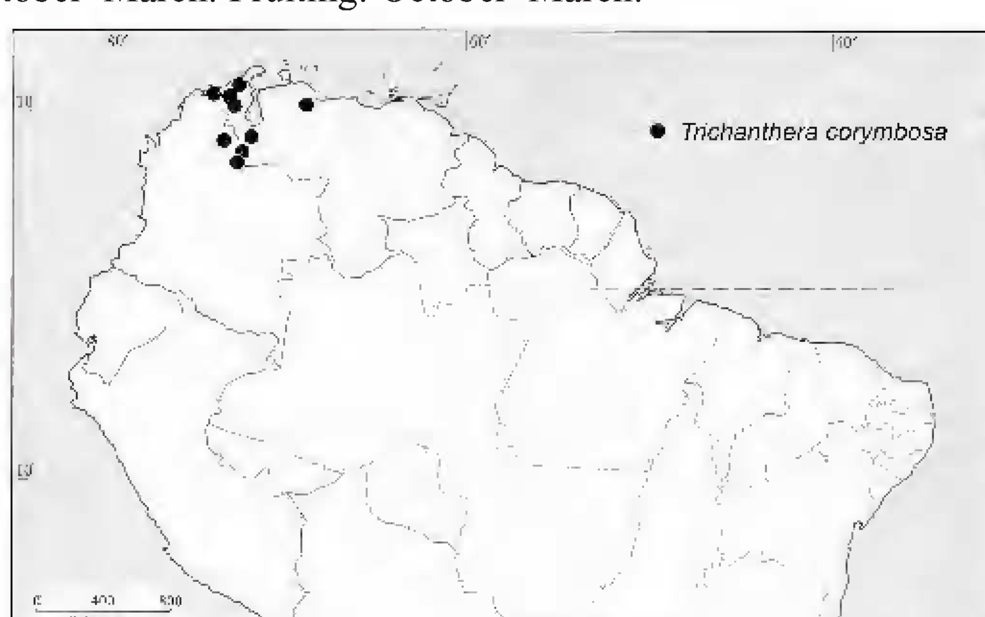

Figure 3. Distribution of *Trichanthera corymbosa*.

Local name.— Yátago (Venezuela; Bono 1996).

Uses.— Planted as living fences along roads and streams in Venezuela (Bono 1996).

Conservation.— *Trichanthera corymbosa* is known from fewer than 20 collections in a limited geographic region (extent of occurrence = ca. 114,900 km^2; area of occupancy with grid cell area of 4 sq. km = 44 km^2; north-south linear distance = ca. 390 km; east-west linear distance = ca. 560 km). Based on the AOO, the species could be considered as endangered (EN) if two subcriteria under criterion B are met. Three geographically isolated subpopulations could be recognized, all of which are potentially threatened by deforestation; thus, a single location for this species is currently proposed. Based on satellite imagery (e.g., Google Inc. 2013), local deforestation is evident for at least five of the 11 mapped collection sites for this species. Thus two of the three subcriteria needed to make an assessment in a threatened category for this species are fulfilled, and a status of EN (B2, a, b) is provisionally proposed for this species.

Morphological variation.— Corollas of *T. corymbosa* are sometimes described as white, whitish, yellow, or flesh-colored. Some of these descriptions possibly refer to the dense covering of whitish trichomes on the external surface. The internal surface is described as white (e.g., *Bunting et al. 12260*), maroon (e.g., *Ruiz T. & López F. 1385*), or purple (e.g., *Pittier 12828*). Thus, as in *T. gigantea* (see below), there appears to be variation in the color of corollas of this species.

As is evident from the description above there is also variation in the pubescence of the androecium in this species. The thecae of *Romero C. 7504* are glabrous whereas they are pubescent (where seen) among other collections. In *Romero C. 10753* the portion of the filaments that is exserted from the corolla tube is glabrous; in *Trujillo & Fernández 16379*, that portion is pubescent with both eglandular and glandular trichomes proximally and glabrous distally. Additional observations on entire androecia in flowers of this species are desirable; based on these observations, however, variation in androecial pubescence of *T. corymbosa* appears similar to that in *T. gigantea*.

Inflorescences of *T. corymbosa* are almost always corymbose; however, in *Trujillo & Fernández 16379* from Venezuela they are elongate (up to 230 mm), like those of *T. gigantea*. Calyx lobes and bracteoles of this collection are like those typical of *T. corymbosa*, in which species this collection is treated here. Overall length of the inflorescence (measured from the first lateral branch bearing dichasia or, if such is absent, then from first dichasium to the apex of the inflorescence, excluding corollas), although often shorter in *T. corymbosa* than in *T. gigantea*, overlaps to an extent that it does not appear to be distinctive for either species. *Bunting et al. 12260* is somewhat unusual by its exceptionally large foliose bracts (to 170 × 80 mm) at the base of the inflorescence and its large bracteoles (to 25 × 5 mm) on the proximal dichasia.

A Colombian collection (*Cañas 810*) shows intermediacy between *T. gigantea* and *T. corymbosa* in calyx length (to 15 mm) and form (lobes slightly heteromorphic with the smaller lobes rounded to acute apically). Bracteoles of this collection are like those of *T. gigantea*, however, in which species this collection is treated. Another collection from Colombia (Norte de Santander: Ocaña, 6000 ft., *Kalbreyer 1264* at K) shows intermediacy between the two species in most of the characters noted in the key. Given the apparent sympatry of these species as noted above, similarity of their flowers, and relative ease of artificial interspecific hybridization demonstrated in several genera of Acanthaceae (e.g., Long 1975 and Daniel 2007 for *Ruellia* L.; Daniel 1983 for *Carlowrightia* A. Gray; Daniel 1984 for *Anisacanthus* Nees; Daniel 1986 for *Tetramerium* Nees), hybridization between the two species of *Trichanthera* might account for the rare instances of intermediacy observed.

Additional specimens examined.— **Colombia: Cesar**: Sierra de Perijá, eastern Manaure, hoya del Río Manaure, San Antonio, *J. Cuatrecasas & R. Romero-Castañeda 25341* (F, US);

Cordillera Oriental, Corregimiento Manaure, Finca Los Venados, *R. Romero-Castañeda 7504* (MO, US). **Magdalena**: de San Pedro a Cebolleta, *R. Romero-Castañeda 10753* (F, MO, NY). **Norte de Santander**: environs de Ocaña, *L. Schlim 135* (BM, K, P).— **Venezuela: Mérida**: vicinity of Tovar, along Río Mocoties, *H. Pittier 12828* (G, NY, US). **Táchira**: Distr. Junín, Las Lajas, entre Delicias y Villa Páez, *L. Ruiz T. & M. López F. 1385* (US). **Yaracuy**: Distr. Bruzual, Mpio. Campoelías, vertiente sur, próxima a carretera Campoelías–La Laguna–Tupe, *B. Trujillo 16021* (MO); Distr. Bruzual, Mpio. Campoelías, La Puente, riachuelo permanente en carretera Campoelías–Tierrita Blanca, km 10, *B. Trujillo & A. Fernández 16379* (MO, US). **Zulia**: Distr. Mara, alrededores de Puesto "El Bosque" de la Guardia Nacional, 10°47′N, 072°40′W, *G. Bunting et al. 12260* (NY, US); Ayapa [Ayapaina], Sierra Perijá, W of Machiques, *Bro. Ginés 147* (US); Sierra de Perijá, a lo largo de la quebrada del Río Omira–Kuná (Tumuriasa), cerca de la frontera Colombo-Venezolana, SW de Pishikakao e Iría, *J. Steyermark et al. 105547* (G, MO, US).

2. *Trichanthera gigantea* (Bonpl.) Nees in A. de Candolle, Prodr. 11:218. 1847. *Ruellia gigantea* Bonpl. in Humboldt and Bonpland, Pl. Aequinoct. 2:75, t. 102. 1810–1811 ("1809"). *Trichanthera gigantea* Bonpl. ex Steud, Nomencl. ed. 1, p. 708. 1821, nom. illegit. (in syn.). *Trixanthera angularis* Raf., Sylva Tellur. 146. 1838, nom. illegit. **Type.**— Colombia. "Habitat frequentissime in sylvis fluvii Magdalenae, prope Badillas et juxta Ybague," (fide protologue), without locality or date (specimen), *A. Humboldt & A. Bonpland s.n.* (lectotype, designated here; see discussion below: P-00719181!). Figure 4.

Clerodendrum verrucosum Splitg. ex de Vriese, Ned. Kruidk. Arch. 1:351. 1848 (as "*Clerodendron verrucosum*"). *Besleria verrucosa* (Splitg. ex de Vriese) Pulle, Recueil Trav. Bot. Néerl. 9:163. 1912. **Type.**— Suriname. "Crescit ad margines fluminum Parae cet. satis frequens," January 1838, *F. Splitgerber 523* (fide Wasshausen, 2006: holotype: L; isotype: P).

Besleria surinamensis Miq., Linnaea 22:471. 1849. **Type.**— Suriname: without locality, *F. Hostmann 764* (lectotype, designated by Wasshausen in 2006: U-image!; possible isolectotypes, see discussion below: MO!, P!, S!).

Trichanthera gigantea var. *guianensis* Gleason, Bull. Torrey Bot. Club 54:617. 1927. **Type.**— Guyana. **East Berbice-Corentyne**: Greale, Corentyne River, Oct 1879, *G. Jenman 371* (lectotype, designated here; see discussion below: K-image!).

Shrubs to trees to 15 (–25) m tall and to 30 (–140) cm in diameter (DBH), often suckering from and/or with prop roots at base, sometimes with multiple trunks, branches sometimes long and pendant; young stems densely pubescent with flexuose to antrorse eglandular trichomes 0.05–0.3 mm long, trichomes sometimes deciduous in patches, mature stems glabrate. Leaves petiolate, petioles to 75 mm long, blades ovate to elliptic 60–310 mm long, 34–150 mm wide, 1.4–2.6 × longer than wide, rounded to acute to subattenuate at base, acute-apiculate to acuminate at apex, surfaces covered with sessile and lenticular glands to 0.05 mm in diameter (sometimes inconspicuous; punctate-glandular), otherwise nearly glabrous and with any trichomes mostly restricted to major veins, margin entire to sinuate. Inflorescence an elongate terminal thyrse or panicle of thyrses, 50–200 mm long, rachis hidden by dense trichomes like those of young stems, dichasia expanded to a greater or lesser degree, pedunculate, peduncles 6–17 mm long, pubescent like rachis, secondary peduncles similar to peduncles. Bracts caducous or persistent, ovate to triangular, 2–5 mm long, 2–3 mm wide, proximal pair(s) sometimes somewhat leaflike and larger, pubescent like rachis. Bracteoles and secondary bracteoles triangular, 2–4 mm long, 1.5–2.4 mm wide. Flowers pedicellate, pedicels 2–8 mm long. Calyx green or purplish (at least distally), 6–13 mm long during anthesis, tube 1–3 mm long, lobes homomorphic, imbricate, ovate-elliptic to elliptic to oblong

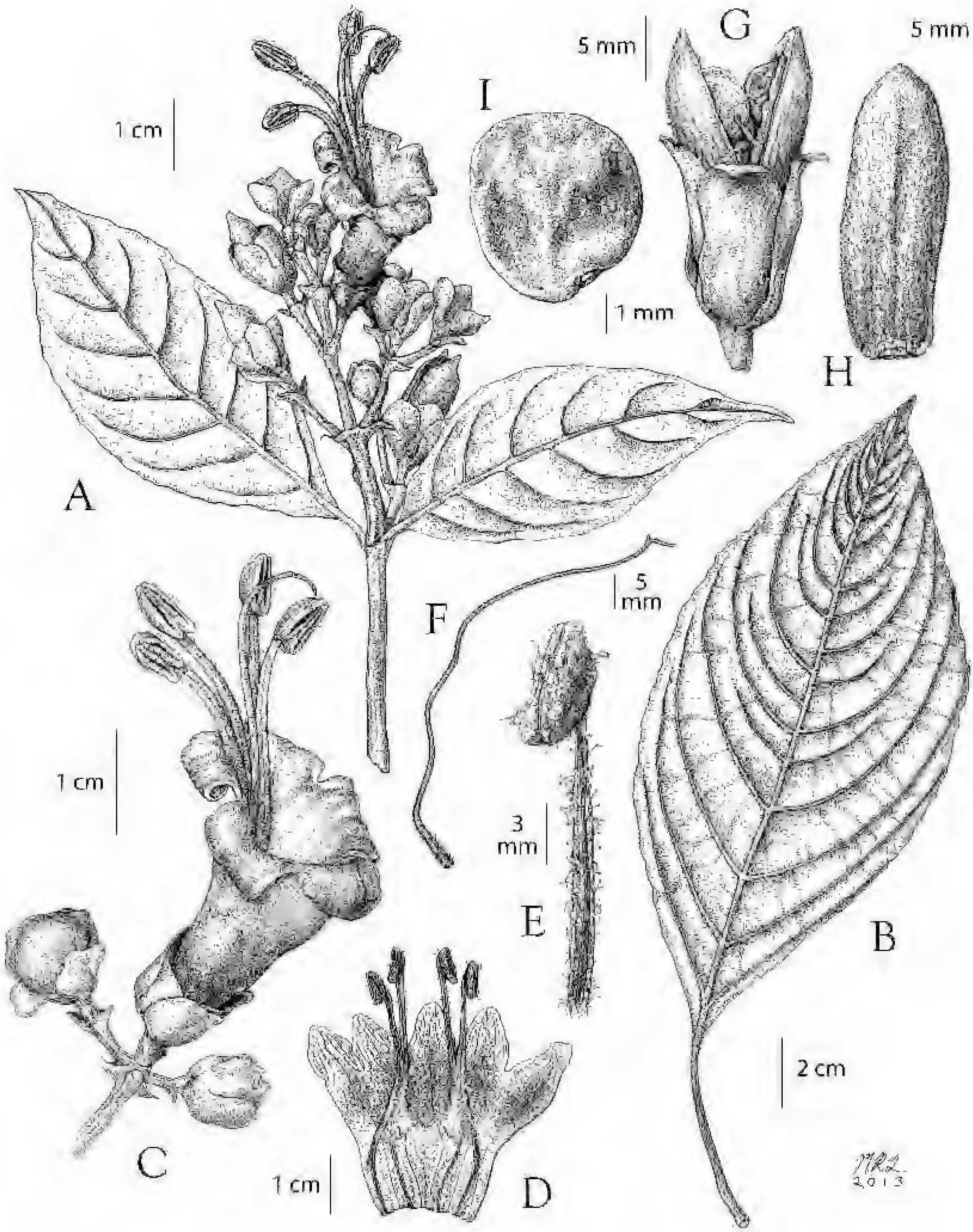

FIGURE 4. *Trichanthera gigantea*. A. Distal portion of branch with inflorescence (*Luteyn & Pipoly 9378*, CAS). B. Leaf from proximal portion of shoot (*McPherson 7081*, CAS). C. Dichasium (*Daniel et al. 5474*, CAS). D. Corolla opened to show stamens (*Daniel et al. 5474*, CAS). E. Stamen (*Daniel et al. 5474*, CAS). F. Style and stigma (*Daniel et al. 5474*, CAS). G. Calyx and capsule (*Daniel & Herrera 5490*, CAS). H. Capsule (*Luteyn & Pipoly 9378*, CAS). I. Seed (*Daniel et al. 5474*, CAS). Drawn by M. Logies.

to obovate-elliptic, 5–11 mm long, 3.5–7.3 mm wide, rounded at apex, abaxial surface punctate-glandular and pubescent with antrorse eglandular trichomes, margin ciliate with erect to flexuose eglandular trichomes to 0.7 mm long. Corolla appearing ± glossy where not covered with trichomes, salmon-colored to dark reddish to brownish red to maroon in throat with lobes similarly colored or often tinged with yellow (along margins or distally) or entirely yellowish internally, 27–45 mm long, externally punctate-glandular and distally densely pubescent with appressed eglandular trichomes (such that the obscured surface appears pale) while lacking eglandular trichomes proximally, narrow proximal portion of tube 7–20 mm long, throat (6.5–) 9–20 mm long, 8–16 mm in diameter near midpoint, limb (15–) 20–30 mm in diameter, lobes often reflexed to recoiled, ovate, 6–11 mm long. Stamens 25–35 mm long, filaments salmon-colored to reddish or maroon proximally and often yellowish distally, pubescent (the longer stamen of each pair more densely so) with glandular (sometimes sparse or inconspicuous) and eglandular trichomes, thecae yellowish, 4.5–7 mm long, pubescent with flexuose eglandular trichomes to 3 mm long and dorsally puberulent with subsessile glands to 0.1 mm long (also on connective), pollen (*Daniel et al. 5474*) 67–79 µm (polar axis) × 63–70 µm (equatorial axis, apertural face) × 40 µm (equatorial axis, interapertural face). Style reddish, 25–47 mm long, pubescent near base, glabrous distally, stigma with 1 lobe 2–4.5 mm long, straight to coiled, other lobe vestigial, 0.3–0.5 mm long. Capsule 16–20 mm long, densely pubescent with antrorsely appressed eglandular trichomes. Seeds 4.5–4.7 mm long, 4–4.3 mm wide.

Phenology.— Flowering throughout the year; fruiting: January–August (and probably other months as well).

Distribution and habitats.— Southern Central America (Panama), northeastern South America (Brazil, French Guiana, Guyana, Suriname, and Venezuela), and northwestern South America (Colombia, Ecuador, and Peru)—occurring from the Province of Veraguas in central-western Panama (ca. 08°7′49.33″N, 080°56′52.89″W) southward to the Amazonian lowlands near Belém in northeastern Brazil (ca. 01°26′55.04″S, 048°22′45.41″W) in the east and to the eastern slope of the Andes in the region of San Martín in north-central Peru (ca. 06°34′7.19″S, 076°18′28.88″W) in the west (Fig. 5); plants occur in swampy ground and agricultural lands (pastures, cafetales), and especially along streams, fencerows, and roadsides in regions of tropical (dry to) moist to wet, lowland to montane, primary and secondary forests at elevations from sea level to 2250 m (to 3500 m *fide* Wasshausen 2013). Because *Trichanthera gigantea* is often cultivated (e.g., as a living fence, or for forage), the anthropogenic distribution of this species is undoubtedly more extensive than that suggested by the localities noted in the specimens cited; collections explicitly indicating that plants were cultivated are not included in that list. The species is especially common (or at least commonly collected) in Colombia. In Venezuela, plants are restricted to two regions on opposite sides of the country—both branches of the Cordillera Oriental in the west and lowlands of the Orinoco delta in the northeast.

The species has been noted to occur as far north as lowlands in Costa Rica (Leonard 1938; McDade 1983; Durkee 1986). The only two specimens from Costa Rica attributed to this species (Leonard 1930), both from Guanacaste in the northwestern part of the country (Tilarán, *P. Standley & Valerio 46569* at US; Nicoya, *Tonduz s.n.* in 1900 at US), are sterile, although *Standley & Valerio 46569* has immature inflorescences. Both appear superficially similar to *Trichanthera gigantea*. However, comparison of these plants to those of *T. gigantea* reveals that they lack the very conspicuous foliar cystoliths, triangular bracts, and feltlike pubescence of the young stems of the latter species. Thus, I remain unconvinced that either of these specimens represents *T. gigantea*, and Costa Rica is excluded from the known geographic range of this species.

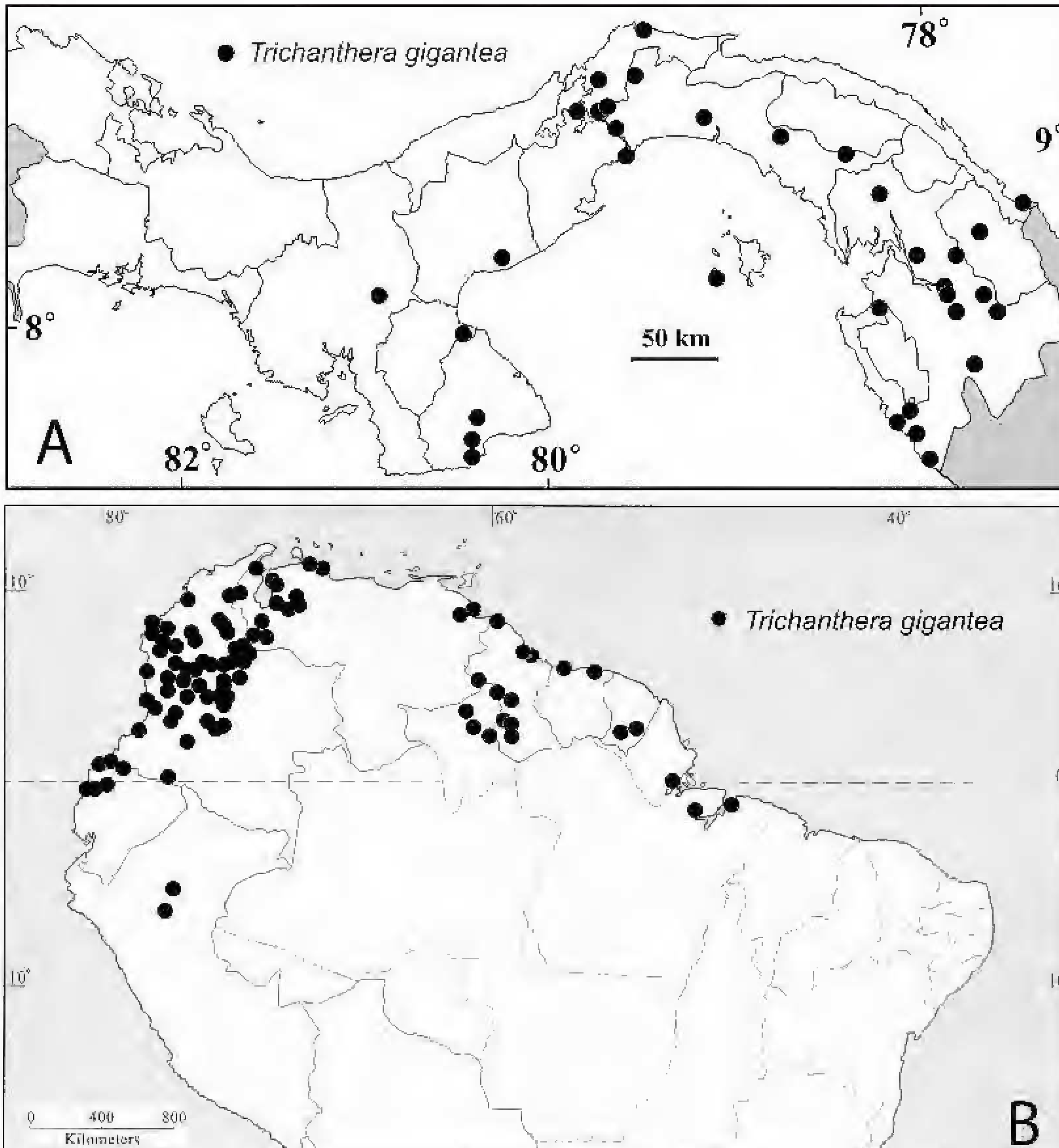

FIGURE 5. Distribution of *Trichanthera gigantea*. A. Distribution in Central America (Panama). B. Distribution in South America.

LOCAL NAMES.— Wasshausen (1992), Record and Hess (1943), and Cook et al. (2005) listed the following local names for the species (including those from countries where it is only cultivated): aro blanco, cajeto, cenicero, fune, madre de agua, nacedero, quiebrabarriga/quiebrabarrigo, suiban (Colombia); tuno (Guatemala); naranjillo (Venezuela); palo de agua (Colombia and Panama); and beque, canella de Garca, pau santo (Brazil). "Nacedero" appears to have the widest usage in both Colombia, where the plant is abundant, and in agricultural literature concerning *Trichanthera gigantea*. Indeed, this name and "cajeto" were listed by Bonpland (1810–1811). Additional local names and their sources from Colombia include: rompebarriga (*Archer 523*); arbol de agua, aro, cafetero, cafeto, chumbaguás, cuchiyuyo/cuchuyuyo, güibán, naceró, paloesal, sanantigua, sietenudos, tumbaguás, yátago, and zanca de araña (Bernal et al. 2013); zanco (*Forero & Jaramillo 461*); and cajón de fraile (*von Sneidern 5698*). Other names encountered on herbarium specimens include: canela de velho (Brazil, *Rabelo et al. 2009*), curuta (Venezuela, *L. Ruiz Terán 458*), janau (Brazil, *Pires 51848*), montonero (Ecuador; *Pennington & de la Cruz 10516*), naiang (Venezuela, *M. Lizarralde 306*), sapote yacu (Peru; *Williams 4894*), and watra-oedoe (Suriname; *Werkhoven & v. Troon UVS 16450*).

Uses.— Leaves and green stems of *Trichanthera gigantea* have been shown to be a useful forage crop in its native geographic range and elsewhere. Numerous studies have documented its ecological parameters for cultivation, nutritive value as fodder, relative usefulness for various domesticated mammals, and harvest times and yields (e.g., Rosales 1997; Cook et al. 2005). Due to the broad ecological tolerance of this species (e.g., see above for ranges in elevation and biotic communities) and ease of propagation from cuttings, it can be grown in diverse habitats (Rosales 1997). Outside of its native range, the species has been grown for its agricultural use in other parts of tropical America, southeastern Asia, and Malesia.

Other uses attributed to this species include: windbreak (Leonard 1930), living fence (e.g., *D'Arcy & Sytsma 14473*; Wasshausen 1992), and cultivated ornamental (Wasshausen 2013). Rosales (1997) indicated that "sprouts" of the species are used in maize porridge for human consumption. The wood is considered to be of relatively low quality (i.e., only suitable for unfinished wood products), but it is used for fuel and to make charcoal (Fern 2014). Wood anatomy of *Trichanthera gigantea* was studied and described by Williams (1928; based on *Pittier 12,056*), Carlquist and Zona (1988; based on Forest Products Laboratory, Madison, Wisconsin sample 1117; likely from *Williams 4894*), and Mennega (2006; Utrecht Wood coll. 175a and 2001). Corothie (1961; without citation of voucher) described wood anatomy of "*Trichanthera* sp." Wasshausen (1992) noted that woodcutters usually leave plants of *T. gigantea* standing to protect springs and streams.

Numerous medicinal uses for *Trichanthera gigantea* have been recorded for humans and domesticated animals. The following uses have been ascribed to humans: infusions of leaves used to treat flu and plants used for treatment of white vaginal discharges (de la Torre et al. 2008; Ecuador); a decoction of leaves used by women in labor to speed delivery (*Lescure 2236*; Ecuador); "en infusión como colagogo y diurético y en cocimiento como antiflogístico" (*Puentes s.n.*; Colombia); used as a remedy for fevers (Wasshausen 1992; Colombia); plants used as a blood tonic, to treat nephritis, and as a lactogenic drink for nursing mothers (Cook et al. 2005); and green stems used to cure nephritis and roots used as a blood tonic (Rosales 1997; Colombia). Medicinal uses for domesticated animals include: leaves used to treat hernias (de la Torre et al. 2008; Ecuador); hot poultices of leaves used to cure abdominal hernias of horses (Wasshausen 1992; Colombia); and plants used to treat colic and hernia in horses, retained placenta in cows, and intestinal obstructions in domestic animals (Rosales 1997; Colombia).

Conservation.— *Trichanthera gigantea* is known from more than 200 collections from a broad geographic area (extent of occurrence = ca. 4,591,000 km^2; north-south linear distance = ca. 1,980 km; east-west linear distance = ca. 3,625 km). Even if the EOO is reduced by one-half to two-thirds to account for open water (marine and terrestrial) and large regions from which the species has not been recorded, the geographic distribution of *T. gigantea* remains quite large, and there would appear to be significant amounts of suitable habitat for this species in much of the region (i.e., the northern and central portions of the Amazon basin) in which it could potentially occur. Based on its wide distribution (both natural and anthropogenic), local abundance (plants are sometimes noted to be common where found, e.g., *Piedad R. et al. 40)*, occurrence in several protected areas in portions of its geographic distribution, and broad ecological amplitude, *T. gigantea* appears to be a taxon of least concern (LC) based on IUCN criteria (IUCN 2014).

Flowers of *Trichanthera gigantea* are reputed to be the major food (nectar) source for the endangered (IUCN category EN) chestnut-bellied hummingbird, *Amazilia castaneiventris*, the abundance of which appears to be affected by the availability of these trees and which exhibits territorial behavior where flowers are common (Cavanzo 2011; BirdLife International 2012). Cavanzo (2011) also noted that reproduction of *A. castaneiventris* was observed in periods of increased floral abundance of *T. gigantea*.

NOMENCLATURE.— According to the protologue of *Ruellia gigantea*, the type locality is in the basin of the Río Magdalena in Colombia. Plants were either collected or noted to occur near Badillas (sometimes cited as "Badillo" or "Badilla," ca. 07°58′20.00″N, 073°51′11.60″W) and in the valley of the Río Combeima near Ibagué at 1300 m (04°27′14.65″N, 075°15′20.15″W). Both Pérez A. (1956) and Wasshausen (1992) noted that Mutis had previously described and illustrated this plant, and that Bonpland had likely made use of these materials. At least five specimens of *Trichanthera gigantea* resulted from Humboldt and Bonpland's trip up the Río Magdalena, and it is likely that there were at least two collections (based on numbers noted in handwritten descriptions of the specimens at P). The known extant specimens are discussed below.

Leonard (1930) indicated that the type locality of *Trichanthera gigantea* was "in sylvis fluvii magdalenae prope Badillas." He subsequently noted that type material of *T. gigantea* was at B and K-Hooker (Leonard 1951), from where specimens had been seen and noted by Nees (1847). The holotype is sometimes cited as having been a specimen destroyed at B (Wasshausen 1992; Wasshausen 2006). Field Museum photo 5887 from the Berlin Negatives database (emuweb.fieldmuseum.org/botany/berDisplay.php?irn=240003&QueryPage=%2Fbotany%2Fsearch_berlin.php) of the destroyed specimen at B reveals that this specimen lacked collection data (at least on the face of the specimen bearing the plant). This specimen was undoubtedly part of the set of collections given to Kunth by Humboldt prior to his return to Berlin in 1829 (Hiepko 2006), and included in the general collection at B. It would have been a duplicate of one of the collections at P, and thus an isosyntype. There are no specimens of *T. gigantea* (under that name or *R. gigantea*) in the Willdenow herbarium at B (Hiepko 1972). Among the major sets of collections of Humboldt and Bonpland (Hiepko 2006), there are three specimens of *T. gigantea* at P (where Bonpland began working up the primary set of their collections prior to Willdenow and subsequently Kunth taking on that task). From the specimens and extensive notes of Bonpland (on at least two of three sheets of paper attached to one of the specimens; these two bear extensive descriptions, which generally correspond to information in the protologue, and are apparently based on collections numbered *1545* and *1828*), it seems reasonable to assume that the original material for this species is at P. At least one of the specimens at P likely was in Bonpland's set that was incorporated into the general herbarium at P in 1832 (Hiepko 2006). Because there are at least two discernible localities in the protologue and undoubtedly at least two different collections, there appear to be syntypes. The specimen from the general herbarium to which all of the descriptive materials are attached, and which is the most complete of those at P, is designated as the lectotype. The other specimens at P, at least one of which could be an isolectoype, are P- Bonpl.-00670081 and P-00719182. A duplicate of one of the Humboldt and Bonpland collections (an isosyntype or an isolectotype) is extant at K.

Neither specimens nor images of types of *Clerodendrum verrucosum* have been seen. The herbaria of deposit noted above is derived from Wasshausen (2006).

From among the syntypes of *Besleria surinamensis* (i.e., *Kappler 1639* and *Hostmann 764*), Wasshasuen (2006) designated *Hostmann 764* at U as the lectotype. The presumed isolectotypes at MO, P, and S indicate Hostmann's number as "764a." Neither the protologue nor the presumed isolectotypes provide place or date of collection. Locality data for the other syntype, *Kappler 1639*, which was collected in 1844, is noted in the specimens cited below. The lectotype is mounted on the same sheet as a specimen of *Kappler 1639* at U.

Gleason (1927) did not designate a type for *Trichanthera gigantea* var. *guianensis*. Among the five collections of *T. gigantea* he cited in the protologue, at least two of them appear to pertain to his new taxon. Leonard (1930) did not indicate a type for var. *guianensis*. Although Wasshausen (2006) cited *Jenman 371* at K as the lectotype of this variety, he did not indicate that it was being designated as such by him and it is not listed among the new lectotypifications made in his treatment (Wasshausen 2006:163); thus, his indication does not constitute a lectotypification (McNeill et al. 2012). Although I searched the literature on Acanthaceae in the region in which this taxon was collected, I did not find a lectotypification for this species conforming to the rules of nomenclature. Thus, I have designated *Jenman 371* at K as the lectotype of *T. gigantea* var. *guianensis*.

Morphological variation.— Gleason (1927:617) noted that *Trichanthera gigantea* var. *guianensis* consisted of lowland plants that differed by their "larger flowers, more hirsute filaments, smaller and more loosely branched inflorescences, and somewhat glaucous leaves, with the veins not elevated on the upper side." Leonard (1930) provided more precise distinctions (inflorescences 3–8 vs. 5–15 cm long and 2–3 vs. 4–5 cm wide, and filaments pilose throughout vs. filaments pilose proximally and glabrous distally), but noted corollas of the same size as those of the nominate variety. He indicated that var. *guianensis* occurs in Brazil, Guyana, and Suriname whereas var. *gigantea* occurs in Colombia, Costa Rica, Ecuador, Panama, Peru, and Venezuela. Bremekamp (1938a, 1938b) did not make reference to this variety in his detailed account of the genus for the *Flora of Suriname*, and his description noted that filaments of plants from Suriname are densely pubescent proximally but glabrescent distally. Most recently, Wasshausen (2006) recognized var. *guianensis* for the plants occurring in Guyana, Suriname, and French Guiana. Based on my studies, similar variation in corolla length, filament pubescence, and inflorescence length is evident among plants in the eastern portion of the species' range (Brazil, Guyana, Suriname), its western range in South America (Venezuela, Colombia, Ecuador), and in Panama. There appears to be some geographic tendencies in pubescence of the filaments. For example, 1) all plants from Ecuador have few or no eglandular trichomes distally on the filaments (but this condition is also evident in other parts of the species' geographic range), and 2) plants from Guyana, Suriname, and Brazil generally have trichomes on the filaments, but these are more abundant in some plants than others (and this variation is also seen elsewhere in the geographic range of the species). Thus, no infraspecific taxa are recognized in this account.

Plants that are somewhat morphologically intermediate with *T. corymbosa*, at least in some characters, are discussed under that species.

Floral biology and pollination.— The following information pertaining to the floral ecology of *Trichanthera gigantea* is based on personal observations, information noted on herbarium specimens, and published studies. The relatively large, somewhat fleshy corollas (Fig. 2) open in the afternoon (Perez A. 1956; pers. obs., *Schmalzel 372*, *Judziewicz 4493*) when nectar is present (Perez A. 1956; *Schmalzel 372*) and detectable odors absent (pers. obs., *Judziewicz 4493*, *Pennington & de la Cruz 10516*, *Piedad R. et al. 40*). Floral rewards include pollen and nectar. Corollas dehisce and fall from the inflorescence before morning of the next day. The style remains attached to the ovary for at least several days following anthesis; ovaries that do not set fruit fall from the plant within three days (McDade 1983). Working at a site in Panama, McDade (1983) demonstrated that flowers are neither autogamous nor apomictic (at least not showing autonomous agamospermy), that at least eight pollen grains are necessary for fruit and seed set, and that mean seed set per fruit was very low at this site, probably because of pollen limitation (low vigor of pollen, low numbers of grains deposited on stigmas, or both).

Pollination of *Trichanthera gigantea* by bats (*Glossophaga soricina*) was documented by Steiner (1981) and photographed by Merlin Tuttle (Anonymous 1984; image can be viewed at: *<http://www.scientificamerican.com/slideshow/bats-in-history-and-world/>* and *<http://www.wbur.org/npr/181634051/this-bat-knows-how-to-drink?ft=3&f=181634051>*). These bats hover in front of flowers, gather nectar with their highly specialized tongues (Harper et al. 2013), and contact stigmas and/or pollen with the top of their heads. Visitation to flowers by bats was also noted on labels of several herbarium specimens (e.g., *Monslave B. 807* from Colombia). Elsewhere among Acanthaceae, bat pollination has been noted for *Harpochilus neesianus* Mart. ex Nees (Acanthoideae: Justicieae) by Vogel et al. (2004). Flowers that share the characteristic syndrome of floral adaptations associated with bat pollination have been noted for several other Neotropical species of *Louteridium* (e.g., Vogel et al. 2004) and *Ruellia* (e.g., Vogel et al. 2004; Ramamoorthy 1991; Tripp 2010).

Other floral visitors to *Trichanthera gigantea* include red wooly opossum (*Caluromys derbianus*; Steiner 1981), hummingbirds (Pérez A. 1956; McDade 1983; Cavanzo 2011, which shows a photograph of *Amazilia castaneiventris* visiting and possibly pollinating a flower of *T. gigantea*; Henry Stockwell in Panama, pers. comm.; *Nee 10446*; *Tripp & Lujan 520*, which indicates hummingbirds as pollinators), large bees (Perez A. 1956; McDade 1983), and ants (Perez A. 1956; Rosales 1997). Some of these floral visitors likely effect pollination as well. Collectors have been particularly attentive to the presence of aggressive ants on inflorescences or flowers of plants (e.g., *Almeda & McPherson 6022, Daniel et al. 5475, Haught 4549, Judziewicz 4493, Luteyn & Pipoly 9378, Phillippe et al. 21186*). The ants have been described as "swarming," "stinging," and "guarding flowers." Some collections note that the ants make "mudlike" nests in the inflorescences.

ADDITIONAL SPECIMENS EXAMINED (only images were seen for specimens cited from CDMB and COL).— **BRAZIL: Amapa**: Macapá, Rio Vila Nova, *B. Rabelo et al. 2009* (NY, US). **Pará**: Belém, igapó do I.A.N., *G. Black 826* (NY, US); IPEAN grounds, Belém, *A. Gentry & A. Pinheiro 13102* (MO, US); Amazon estuary, Breves, *E. Killip & A. Smith 30230* (F, NY, US); Crauateua, Rio Guamá, *R. de Lemos Fróes 20392* (NY, US); beira do Guamá, *J. Pires 3454* (CAS, US); vic. of Belem, *J. Pires 51848* (NY, US); Belém, R. Guamá, *N. Silva 57808* (NY, US). **Roraima**: Mun. Alto Alegre, Reserva Ecológica de Maracá, N tip of island at Três Igaripés, Corredeira de Rapariga, ca. 1 km upriver from jct. Furo de Santa Rosa with Rio Trairão, *P. Edwards 2649* (C, MO, NY, UPS); Canto Galo, Rio Mucajaí between Pratinha and Rio Apaiú, *G. Prance et al. 3980* (CAS, NY, S, US); 10 km SE of Serra de Lua, 02°25–29′N, 060°11–14′W, *G. Prance et al. 9336* (NY, S, US).— **COLOMBIA: Antioquia**: 0–5 km S of Q. La Tirana along the river, vic. Planta Providencia, 28 km S of Zaragoza, *W. Alverson et al. 328* (MO, NY, WIS); 4 km N of Fredonia, *W. Archer 523* (NY); Mpio. Frontino, San Andrés, vía Dabeiba–Fuemia, 18–33 kms., 06°40′N, 076°23′W, *R. Callejas et al. 5850* (MO, NY, US); Mpio. Chigorodó, 2 km E of Chigorodó, Had. Pasatiempo, 07°40′N, 076°42′W, *R. Callejas et al. 9721* (NY); Mpio. Cocorná, La Piñuela, carretera a San Francisco, 06°02′N, 075°08′W, *D. Cañas 810* (MO); Mpio. San Luis, camino de la vereda Las "Confusas" a la autopista Medellín–Bogotá, 06°00′N, 074°45′W, *D. Cárdenas L. & J. Ramírez 2570* (COL, MO); Parque Nacional Natural "Las Orquideas," Sector Venados, margen derecha del Río Venados, 06°33′N, 076°19′W, *A. Cogollo et al. 3010* (COL); near Río León, ca. 20–30 km upstream and S of river mouth and ca. 15 km W of Chigorodó (ca. 07°45′N, 076°50′W), *C. Feddema 1917* (MICH, NY, US); Pavarandó Grande, Río Pavarando, *R. Fonnegra et al. 1716* (MEXU, MO, NY, US); Mpio. Río Negro, 7 km from Turbo on road to Necocli, 08°9′0″N, 076°41′48″W, *A. Gentry 9223* (COL, MO, NY, US); Turbo, 10 km E of Turbo, *O. Haught 4549* (P, US); cerca de Villa Arteaga, *F. López & M. Sánchez M. 61* (NY); de Puerto Bélgica por la carretera hasta el Río Man, *R. Romero-Castañeda 2333* (COL); Andes, carretera Andes–Jardín, 05°40′N, 075°55′W, *D.*

Sánchez et al. 1155 (MO); vic. of Medellín, *R. Toro 78* (NY); Mpio. Carepa, 2 km N of Carepa, 07°52′N, 076°42′W, *J. Zarucchi et al. 5005* (MO, NY); Mpio Andes, km 13 of road Jardín–Andes (3 km before Andes), 05°39′N, 075°52′W, *J. Zarucchi et al. 7023* (COL, MO, US). **Bolívar**: 1 km de Arenal, *E. Forero & R. Jaramillo 461* (NY); Sahagun, *F. Pennell 4101* (NY); Mpio. Barranco de Loba, corr. El Pueblito, sector Las Payayas, 08°40′N, 074°10′W, *F. Roldán et al. 1837* (NY); Cordillera Occidental, Guimarí, *K. von Sneidern 5698* (PH). **Boyacá**: Mpio. Puerto Boyacá, Inspección de Puerto Boyacá, Quebrada La Cristalina, 05°50′60″N, 074°19′60″W, *R. Bernal et al. 2247* (COL); Mpio. Santa María, Arrayanes, Puerto de Agua Caliente, en la ruta a San Luis de Gaceno, cercanias del Río Lengupá, 04°50′57.8″N, 073°13′45.3″W, *J. Betancur et al. 11530* (COL); Mpio. Zataquirá, Hormigas, *A. Cadena G. 237* (COL); Valle de Soatá, *J. Cuatrecasas & H. García B. 1085* (COL). **Caquetá**: Mpio. San Vicente del Caguán, Trazado de la carretera entre Neiva y San Vicente, Las Perlas, bajo Río Pato, Finca Galicia, *J. Betancur et al. 2276* (COL, MO, US). **Casanare**: Mpio. El Yopal, *J. Campo K. & L. Pinzón P. 208* (COL). **Cauca**: Mpio. Guapi, Parque Nal. Natural Isla de Gorgona, camino a Playa Blanca, *G. Lozano et al. 5641* (COL). **Cesar**: Poponte, Magdalena Valley, *C. Allen 876* (MO). **Chocó**: Mpio. Acandí, Corregimiento San Francisco, Golfo de Urabá, 08°23′N, 077°07′W, *J. Betancur et al. 1216* (MO); Mpio. Acandí, corr. Triganá, Reserva Zazardí, 08°20′N, 077°10′W, *F. Cardona N. et al. 1641* (NY); Mpio. Quibdó, Corregimiento Bebará, sector La Calle en el Río Bebará, *W. Córdoba 411* (MO); Río Chintado, above La Nueva, *J. Duke 9850* (MO); Río Yuto between Lloró and La Vuelta, *A. Gentry & E. Rentería A. 24340* (MO); Río Mecana, 06°16′N, 077°21′W, *A. Juncosa 1745* (MO); Mpio. Quibdó, barrio Bahia Solano, *R. Moreno et al. 5* (MO); Río Tolo, región de Guayabal, al SE de Acandí, *L. Quiñones et al. 4* (COL, MO, US); Parque Nacional Natural Los Katíos, sector Bijao, *S. Zuluaga R. 785* (COL). **Córdoba**: Mpio. San Antero, Cerro de Buenos Aires, 09º17’48.6″N, 075°50’02.9″W, *J. Aguirre S. et al. 181* (COL); Mpio. Lorica, Corregimiento Nariño, Quebrada Cardozo, *O. Rivera D. et al. 1729* (COL); Mpio. Chima, Corregimiento Sitio Viejo, El Cerro, Cerro Tofeme, 09°04′58″N, 075°35′13″W, *O. Rivera D. et al. 2534* (COL). **Cundinamarca**: Caqueza in descendu And. bogotens. orienteus versus, *E. André 1875* (P); Sierra de Subia, 10 km N of Cumaca on road to Viotá, *A. Barclay et al. 3527* (COL, US); Mpio. La Mesa, carretera de La Mesa a Anapoima, El Placer, *A. Fernández & L. Mora 1373* (COL, NY); Mpio. Arbeláez, 7 km antes de Pandi, *J. Fernández A. et al. 7007* (COL, NY); Mpio. Viotá, La Victoria, Finca El Retazo, *J. Jácome 437* (COL); Mpio. Sasaima, Río Agua Dulce, Quebrada Doroga, *G. Lozano C. 654* (COL); Mpio. Viotá, Las Palmas, Finca Pensilvania, *A. Rodríguez A. 3* (COL); La Mesa, vía La Mesa–San Javier, *A. Salama et al. 251* (COL); Mpio. El Colegio, Inspección El Triunfo, La Soledad, desvío por El Quiosco, *A. Sanabria G. et al. 388* (COL); Mpio. Nilo, Inspección de Pueblo Nuevo, camino al Cerro del Cualamaná, *J. Torres R. et al. 774* (COL); entre La Mesa et le Magdalena, *J. Triana s.n.* (NY, P); Santandercito, a orillas del Río Bogotá, *L. Uribe U. 334* (COL); Pradilla near San Antonio de Tena, *J. Wood 4137* (COL, MEXU, US). **Huila**: along river, E of San Antonio Fortalecillas, *E. Little 7930* (UC); Mpio. La Argentina, El Progresso, 02°12′40.1″N, 075°56′40.1″W, *G. Silva et al. GAS0358A* (COL). **Meta**: floodplain of Río Metica just E of Puerto López, 3°55’43″N, 73°2′44″W, *G. Davidse & F. Llanos 5470* (COL, MO, US); caños cercanos a Villavicencio, *J. Fernández A. et al. 5573* (MO); P.N.N. Tinigua, Serranía Chamusa, Centro de Investigaciones Primatológicas La Macarena, *P. Stevenson 922* (MO). **Norte de Santander**: región de Sarare, hoya del Río Chitagá, en La Cabuya, *J. Cuatrecasas 13437* (COL, US); Culagá Valley, near Tapatá (N of Toledo), *E. Killip & A. Smith 20504* (NY, US); W side of Culagá Valley, N of Labateca, *E. Killip & A. Smith 20534* (NY, US); between Chinácota and La Esmeralda, *E. Killip & A. Smith 20891* (US); km 20 carretera via Pamplona, *D. Villamizar V. 72* (MO). **Putumayo**: Río Putumayo, Puerto Porvenir, arriba de Puerto Ospina, hacia La Loma, *J. Cuatrecasas 10733* (COL). **Quindío**: Mpio.

Calarcá, La Bella, km 4 vía Calarcá–Barcelona, 04°30′03″N, 075°41′02″W, *M. González 141* (COL); Mpio. Filandia, El Placer vía a Filandia, *L. Piedad R. et al. 23* (COL); Mpio. Génova, Finca El Janeiro, *L. Piedad R. et al. 40* (COL). **Santander**: 10 km N de Bacaramanga, *J. Araque M. & F. Barkley 18S.212* (NY, US); Mpio. Suaita, Corregimiento San José de Suaita, zona cercana a la quebrada La Vega, *J. Fernández-Alonso et al. 20862* (COL); Mpio. Floridablanca, predios del campus del la Universidad Pontificia Bolivariana, *E. García & J. Benavides 3835* (CDMB); Oiba, *F. González 3591* (NY); Bucaramana and vicinity, *E. Killip & A. Smith 15452* (NY, US); Río Suratá valley , between El Jaboncillo and Suratá, *E. Killip & A. Smith 16426* (US); La Corcova (Tona), *E. Rentería et al. 692* (NY); alrededores de Oiba, *R. Puentes s.n.* (COL); Río Servita, vic. Málaga, *J. Wood 4338* (COL). **Tolima**: El Fresno, *J. Cuatrecasas 9374* (COL); Ibagué, *I. Holton s.n.* in 1853 (NY); Mpio. Ibagué, Tres Esquinas, 04°29′6″N, 075°15′51″W, *A. López 4* (COL). **Valle de Cauca**: Río San Juan, *E. Core 1501* (US); Cordillera Occidental, vertiente occidental, hoya de Albán, entre Quebradita del Retiro y el Río Albán, *J. Cuatrecasas 22631* (F); El Frejito, *E. Dryander 47* (US); Cali, *H. Garcia B. 4314* (US); Mpio. Ginebra, Inspección de Policia, Costa Rica, Mina la Emilia, *L. Jiménez et al. 06* (COL); Bajo Calima, Concesión Pulpapel/Buenaventura, 03°55′N, 077°W, *M. Monslave B. 807* (MO, US); “La Manuelita,” Palmira, *F. Pennell & E. Killip 6193* (NY); cerca de Cali, *E. Pérez A. & J. Cuatrecasas 6332* (COL, US); Timba, *K. von Sneidern 1240* (NY).— **Ecuador: Carchi**: between Chical and Peña Blancas, valley of Río San Juan on Colombian border, *A. Gentry & G. Shupp 26496* (MO); environs of Chical, 12 km below Maldonado on Río San Juan, 01°04′N, 078°17′W, *M. Madison et al. 4474* (F, MO); below Maldonado, ca. 80 km W of Tulcan, *T. Pennington & R. de la Cruz 10516* (US); Maldonado, *L. Werling & S. Leth-Nissen 420* (NY). **Esmeraldas**: Limones–Borbón, 5 km before Borbón, 01°07′N, 079°00′W, *L. Holm-Nielsen et al. 26040* (MO, NY); Macedonia, Esmeraldas–Atacames, *C. Játiva & C. Epling 466* (NY, UC, US); Atacames, 25 km SW de Esmeraldas, *E. Little & R. Dixon 21002* (NY, US); San Lorenzo Cantón, Reserva Etnica Awá, Centro Ricaurte, 01°10′N, 078°32′W, *G. Tipaz et al. 2223* (MEXU). **Los Ríos**: Río Palenque Biological Station, km 56 Quevedo–Santo Domingo, *C. Dodson 5846* (MO, US). **Manabí**: El Recreo, *H. Eggers 14823* (MA, US); 5 km E de Chone, carretera hacia Santo Domingo de los Colorados, 00°40’S, 080°05′W, *D. Neill & M. Asanza 7979* (MO). **Santo Domingo de los Tsáchilas:** near Santo Domingo, *C. Jativa & C. Epling 530* (NY, UC, US); carretera Quito–Chiriboga–Empalme, entre kms. 75 and 85, 00°15′S, 078°50′W, *V. Zak & J. Jaramillo 2326* (RSA, MEXU, MO, NY, US). **Without locality**: *A. Gilmartin 221* (MO).— **French guiana: Cayenne**: Rivière Camopi, en amont du Saut Yaniwé [ca. 03°5′20″N, 052°45′11.69″W], *J. de Granville 2071* (U). **St. Laurent du Maroni**: Saut Pierkourou sur le Tampok [ca. 02°49’59.88″N, 053°33′0.03″W], *Moretti 1268* (P).— **Guyana: Barima-Waini**: Anabisi River, *J. de la Cruz 1348* (NY, US); Hossororo, near Port Kumaka via Aruka River, 08°10′07″N, 059°48′17″W, *T. Hollowell et al. 453* (MO); Barima River, *G. Jenman 7037* (K-image, NY). **Cuyuni-Mazaruni**: Mazaruni Station, *Forest Dept. of British Guiana F624 (3360)*(NY); Roraima, *Schomburgk 998* (P). **Demerana-Mahaica**: E bank of Demerara River at Atkinson Field, *H. Irwin 167* (US); Canaan, Demerara River, *Jenman 5356* (K, NY). **Essequibo Islands-West Demerara**: Naamryck Canal, ca. 3.5 km SW of Parika, 06°50′N, 058°27′W, *L. Gillespie & D. Gopaul 1042* (US); Naamrye Canal just W of Lookout, 06°50′N, 058°25′W, *J. Pipoly & G. Samuels 11752* (NY, P, US). **Potaro-Siparuni**: ca. 0.5 km from Paramakatoi, trail to Youwang and Monkey Mt., 04°41′N, 059°42′W, *H. Clarke & S. Grose 1261* (NY, US). **Upper Takutu-Upper Essequibo**: Rupununi area, Surama, 04°05′N, 059°04′W, *P. Acevedo et al. 3389* (MO, NY, US); Essequibo, South Rupununi savanna, SE of Aishalton, 02°25′N, 059°10′W, *T. Henkel & R. James 3723* (MO, NY, US); NW Kanuku Mts., 2–4 km N of Nappi Mt., 03°19′N, 059°33′W, *B. Hoffman & R. Foster 3597b* (MO); S Pakaraima Mts., 3 km E of Tipuru village, 04°12′N, 059°32′W, *B. Hoffman &*

R. Jacobs 1147 (NY, US); Rupununi Distr., Kanuku Mts., Crabwood Cr., Camp 23, 03°07′N, 059°06′W, *M. Jansen-Jacobs et al. 3300* (MO, NY, P, US); NW slopes of Kanuku Mts., drainage of Moku-Moku Creek (Takutu tributary), *A. Smith 3405* (MO, NY, P, US).— **Panama: "Canal Zone**:" without locality, *P. Allen 1725* (MO, NY); without locality, *M. Correa A. et al. 1719* (MO); Madden Forest Road 2, *T. Croat 8957* (MICH, MO). **Coclé**: lower portion of valley along R. Antón, El Valle de Antón, *A. Hunter & P. Allen 385* (MO). **Colón**: Juan Mina Plantation, Río Chagres, region above Gamboa, *P. Allen 4106* (MO); Boyd-Roosevelt Hwy., 5 mi W of Sabanitas, *T. Croat 14073* (MO, NY, RSA, UC, US); vic. of Río Indio on road from Portobelo to Nombre de Dios, *T. Croat 33620* (MO, NY); along Pipeline Road, 1–5 km NW of Gamboa, 09°08′N, 079°42′W, *E. Judziewicz 4493* (MO, WIS); Chagres River, ca. 3 mi above Gamboa Bridge, *H. Kennedy et al. 2302* (MO, RSA); Parque Nacional Soberania (Pipeline Road), 3–7 km NW of Gamboa, *L. McDade 542* (CAS); along Pipeline Road, 3.5 km NW of Gamboa, *M. Nee 10446* (MO, RSA, US). **Darién**: Serranía de Pirre, near Cana mining camp in region of Alturas de Nique on road to Boca de Cupe, *F. Almeda & G. McPherson 6022* (CAS, NY); vicinity of Canglon, 110 mi from Bayano Dam Bridge, *T. Antonio 4578* (MO); trail from Punta Guayabo Grande to Río Jaque, *T. Antonio & W. Hahn 4432* (MO); without locality, *N. Bristan 124* (MO, UC); Rancho Frio Station, Río Perrecénega, ca. 10 mi E of El Real, *W. D'Arcy & G. McPherson 16165* (MO); 10 km NE of Jaque, Río Tabuelitas above Birogueirá, village on Río Jaque below mouth of Río Pavarandó, *W. D'Arcy & K. Sytsma 14473* (MEXU, MO); 1–5 mi downstream from El Real, *J. Duke 4924* (MO, UC, US); Cerro Piriaque, *J. Duke 8110* (MO); 18 km SE of Jaqué, Ensenada del Guayabo, *N. Garwood et al. 93* (MEXU, MO); Ensenada del Guayabo, 16–19 km SE of Jaqué, *N. Garwood 1201* (MO); Río Tuira between Río Paya and Río Cube, *A. Gentry 4354* (MO); El Real, trail to Río Pirre, *H. Kennedy 2828* (F, MO, NY); trail from Canglón–Yaviza road to Río Chucanaque, 7.7 mi E of Canglón, 08°20′N, 077°50′W, *S. Knapp & J. Mallet 3965* (CAS, MEXU, MO); S of El Real along trail at base of Cerro Pirre, ca. 08°00′N, 077°45′W, *G. McPherson 7081* (CAS, MO); Sambú River above tide limit, *H. Pittier 5541* (NY); El Real airport, *O. Sexton 260* (MO), *261* (MO); Cerro Piriaque, *E. Tyson et al. 3814* (MO); Rio Cocalito, *C. Whitefoord & A. Eddy 118* (MEXU, MO). **Emberá**: Marraganti and vicinity, *R. Williams 1007* (NY). **Herrera**: El Barrero de Pesé, *M. Rodríguez 53* (MO, NY). **Los Santos**: vicinity of Tonosí along Quebrada Ocho Paso tributary of Río Tonosí, *W. Stern et al. 1834* (MICH, MO, US); 10 mi N of Tonosí, *E. Tyson et al. 2948* (MO); road from Tonosí to Guánico, *E. Tyson et al. 3118* (MO). **Panamá**: drowned forest of upper Río Pequeni between Salamanca Hydrographic Station and Río Boquerón, *P. Allen 17275* (MICH, MO, P); Río Villalobos–Pedregal, *D. Botello 26* (MO); Barro Colorado Island, *T. Croat 4632* (NY), *8528* (MO, NY, RSA, US); Río Maje, ca. 30 minutes by speedboat from confluence with Río Bayano, *T. Croat 34378* (MO); along Pipeline Road between entrance to Parque Nac. Soberania and fourth bridge, *T. Daniel & H. Herrera 5490* (CAS, MO); along road to Farfan Beach just W of Bridge of the Americas, *T. Daniel et al. 5474* (CAS, MICH); Barro Colorado Island, *R. Dressler 3427* (MO); between Río Pacora and Chepo, *J. Dwyer et al. 5124* (CAS, MO, US); Barro Colorado Island, *R. Foster 1680* (F, MO); Pipeline Road, 09°15′N, 079°45′W, *C. Hamilton et al. 3253* (MEXU, MO); San José Island, Camp Valley, *I. Johnston 679* (MO, P, US); along Gaillard Hwy., 1.5 km NW of Summit Garden, *M. Nee 9392* (MO, NY); Barro Colorado Island, *R. Schmalzel 372* (MEXU, MO); ca. 15 km SW of Cañaza near Río Torti, base of Serranía de Cañazas, 08°52′N, 078°22′W, *B. Stein 1365* (MEXU, MO); Barro Colorado Island, *W. Stoutamire 2092* (MICH). **Guna (San Blas)**: W side of Loma Armila, *W. D'Arcy & G. McPherson 16133* (MO). **Veraguas**: Santiago, Loma de Regina, *I. Gordon & F. Camarena 43* (MO); Santiago, *L. Urriola 30* (MO).— **Peru: Loreto**: lower Río Huallaga, Santa Rosa [155–200 m], *L. Williams 4894* (US). **San Martín**: prope Tarapoto, Peruviae orientalis, *R. Spruce 3951* (K, NY, P, US).— **Suriname: Commewijne:**

Plant. Liberté, *J. Florschütz & P. Florschütz 1007* (NY). **Nickerie**: Wageningen I, km 172, *M. Werkhoven & F. v. Troon USV no. 16450* (US). **Paramaribo**: ad margines sylvarum pr. u. Paramaribo, *A. Kappler 1639* (MO, P, S). **Wanica**: Domburg, fluv. Suriname inferior, old plantation, *K. Kramer & W. Hekking 2349* (NY); bank of Para River, 2–4 km S of Houttuinen, *K. Kramer & W. Hekking 2748* (DAV, NY).— **Venezuela: Barinas**: las afueras de Puntax de Piedras, *Bernardi 1099* (NY); ca. 34 km NE of Altamira and 5 km NE of Caldas, ca. 08°55′N, 070°20′W, *J. Luteyn & J. Pipoly 9378* (CAS, MO, NY, US). **Delta-Amacuro**: medio Río Grande, 60 km NE de El Palmar, ca. 08°25′N, 061°45′W, *G. Aymard C. 5378* (MO); Dept. Tucupita, 13–14 km SE of Piacoa, along trail to Río San José, 8°32′N, 62°3′W, *G. Davidse & A. González 16453* (MEXU, MO); Dpto. Antonio Díaz, Cano Merejina, 08°46′N, 061°10′W, *A. Fernández 3990* (MO, NY). **Falcón**: Mpio. Jacura, Distr. Acosta, base del Cerro de La Mina, *L. Ruiz T. 458* (MO); Distr. Colina, Río Ricoa, S de Las Dos Bocas, 11°19′N, 069°24–25′W, *J. Steyermark & A. Gonzáles 113647* (MO). **Lara**: road from Guarico to Chabasaquén, 09°35′8.5″N, 069°50′54.3″W, *E. Tripp & M. Lujan 520* (CAS, RSA). **Mérida**: Zea, *Bernardi 1051* (MEXU, NY); San Cristoval, *N. Funck & L. Schlim 1506* (P); Río Caparo, ca. 1 km upstream from dam site, ca. 07°41′N, 071°28′W, *R. Liesner & A. González 9393* (MEXU, MO, US); 0.5–2 km above dam site on Río Guaimaral, ca. 07°45′N, 071°29′W, *R. Liesner & A. González 10578* (MEXU, MO, NY, US); carretera Santa Cruz de Mora–El Portón, *L. Valverde et al. 1119* (MO). **Portuguesa**: Distr. Guanare, terrenos de la UNELLEZ, 09°04′N, 069°49′W, *G. Aymard 1030* (MO); 30 km (air) W of Guanare, along Río Tucupido, 09°2′N, 070°01′W, *R. Liesner et al. 12460* (MEXU, MO, NY, US); NW of Guanare on Río Guanare, 09°2.55′N, 069°48.38′W, *L. Phillippe et al. 21186* (MO); Paso del Guanare, *H. Pittier 12056* (NY); Mpio. Mesa de Cavacas, Distr. Guanare, el lecho del Río Guanare, tramo ca. 1 km desde el Puente de la carretera Guano–Barinas, *B. Stergios et al. 7898* (MO, NY); Río María, Boca del Monte, 23 km N del vado del Río Suruguapo, 38 km N por la autopista Guanare–Ospino, en el sitio Las Marías, N de Guanare, 09°18′N, 069°43′W, *J. Steyermark et al. 127152* (MO, US). **Táchira**: near Palo Grande, *A. Alston 7097* (NY). **Trujillo**: entre Campo Elías y Batatal, *C. Benítez de Rojas 976* (F). **Zulia**: límite Distr. Bolívar-Baralt, Río Misoa, 10 km SE del empalme de las carreteras Maracaibo– Carora–Valera, *G. Bunting & L. Aristeguieta 5175* (NY); Distr. Bolívar, Cuenca de la Represa Burro Negro (Pueblo Viejo), 12 km de la vía Campo Lara–Piedras Blancas–Río Chiquito, *G. Bunting et al. 7204* (NY); Sierra de Perijá, 3.8 km 50° of Saimadodyi, 09°36′N, 072°55′W, *M. Lizarralde 306* (MO, NY); near Riocito [10°34′59.72″N, 072°22′0.06″W], *C. Mell s.n.* in 1923 (NY).

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